

AN APPARENTLY HETEROSPOROUS PLANT FROM THE MIDDLE DEVONIAN OF NEW BRUNSWICK

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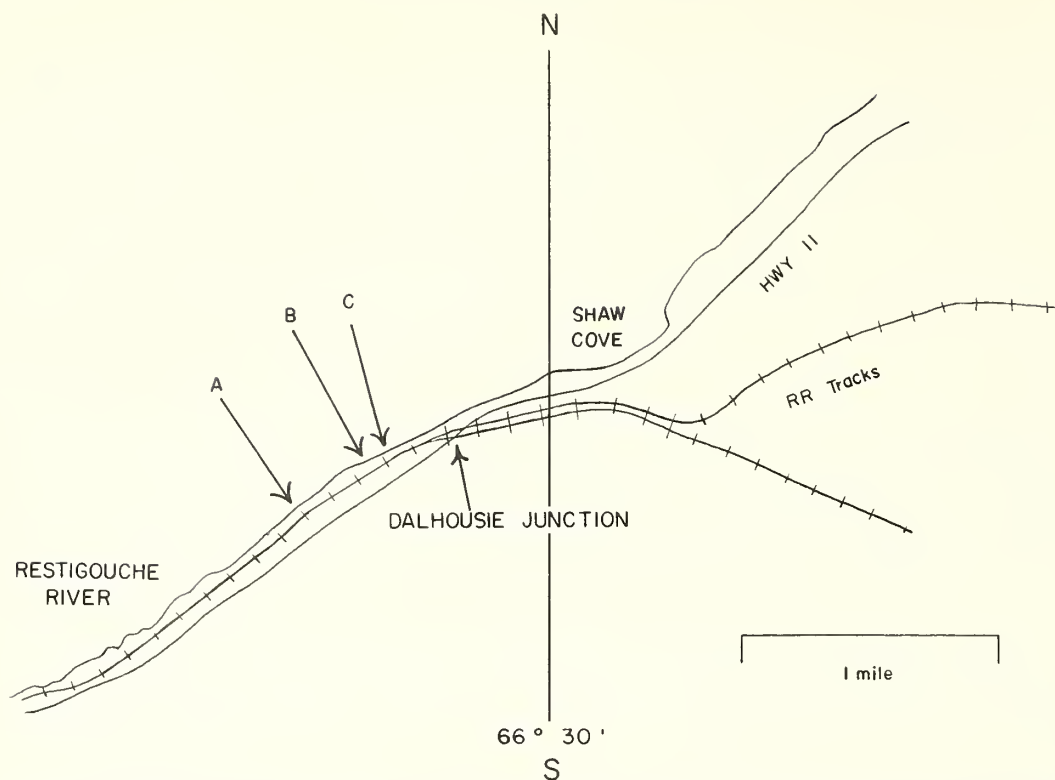
ABSTRACT. A new plant of Lower or Middle Devonian age is described from Chaleur Bay, New Brunswick, as a new genus and species, *Chaleuria cirrosa*. It consists of a main axis bearing closely spiralled monopodial branches which in turn bear spirally arranged dichotomous ultimate branchlets. Pairs of sporangia terminate some ultimate branchlets. Macerations of sporangia yielded spores of two sizes (30–48 μm and 60–156 μm) which also differ from one another in shape and ornamentation. Our evidence suggests that the sporangia contained predominantly large or predominantly small spores or a mixture of both. We suggest that the spores of *Chaleuria* are sufficiently distinct to be considered as megaspores and microspores and that the plant presents evidence of an apparently early stage in the evolution of heterospority.

It is our purpose here to describe well-preserved specimens of a compression fossil representing a new genus of vascular plants, *Chaleuria cirrosa*, from the Middle Devonian of New Brunswick, Canada. It presents, to the best of our knowledge, the earliest evidence of heterospority based on megafossil remains that has been reported to date.

The rocks exposed along the shorelines of Gaspé Bay, Quebec, and the north and south shores of the lower Restigouche River (Quebec and New Brunswick respectively) have long been known to be rich in fossil plant remains, Lower, Middle, and Upper Devonian horizons all being represented. The cliffs in some places are being eroded rapidly, exposing new plant deposits each year and there are many miles of shoreline that merit frequent prospecting. The collecting trips that we have conducted in the past four years (1970–1973) have yielded several new plants and more complete data on some previously described ones. It is evident that the area holds great potential for increasing our knowledge of Lower and Middle Devonian plant life.

LOCALITY AND STRATIGRAPHY

A rather detailed notation on the locality from which our plant was collected is necessary for reasons that will be evident. In July 1972 we devoted several days to prospecting and digging along a few hundred yards of beach outcrop on the south side of the lower Restigouche River, as shown in the accompanying map (text-fig. 1). At a point one-quarter of a mile west from the crossing of the railway and highway No. 11 at Dalhousie Junction there is a narrow cart road that descends to the beach in a westerly direction. From this point extending westward for about one-half mile there are several outcrops along the bank immediately above the normal high-tide mark. We obtained an abundance of fossil plant material here, the most



TEXT-FIG. 1. Map of Dalhousie Junction area, New Brunswick, showing collection localities. Specimens of *Chaleuria* were obtained from Locality A. (From Oak Bay and Escuminac maps of Restigouche County, New Brunswick, Department of Natural Resources.)

productive spots being shown as 'A', 'B', and 'C' on the map in text-fig. 1. *Chaleuria* was found at point 'A'.

In the Chaleur Bay area map (map 330A) that accompanies Alcock's 'Geology of Chaleur Bay' (1935) this half-mile strip is included in the Bonaventure Formation of Carboniferous age. It has been recognized, however, that this is probably incorrect (personal communication from Hugo R. Greiner, University of New Brunswick, to William H. Forbes). The light brown to grey sandy shales of this narrow coastal strip are in striking contrast to the coarse red sandstone of the surrounding Bonaventure Formation. As to the fossils, in addition to *Chaleuria*, we found *Psilophyton*, *Drepanophycus*, *Kaulangiophyton*, and at least one other plant that probably represents a new genus. The assemblage indicates an age not younger than Middle Devonian. It may also be noted that the spores of *Chaleuria* are comparable to spores reported from both Lower and Middle Devonian strata in North America and Europe. In addition we have found in our macerates the spore genus *Emphanisporites* which is known to be extremely abundant in the Lower Devonian and present in the Middle Devonian; ours are similar to *E. rotatus*, a common Lower Devonian spore.

On the Escuminac Sheet map of Bonaventure County, Quebec (Canadian Geological Survey map 286A, for 1936), there is a patch of the Middle Devonian Gaspé sandstone outcropping along the coast about three-quarters of a mile east of Dalhousie Junction and two other small patches between Pin-sec-Point and Peuplier Point. Since the particular area that we are concerned with (text-fig. 1) is, for the most part, densely covered with vegetation down to the beach it is not surprising that it was overlooked in Alcock's account of 1935. Thus, on the basis of the lithology and the fossil plant content, we consider the strip as belonging to the Campbellton Formation of the Gaspé sandstone and not younger than Middle Devonian.

At the point marked 'A' on our map the rock consists of a fine to medium-grained, grey to greenish-grey argillaceous sandstone; it is generally well sorted and small quantities of muscovite are present. The beds dip at an angle of about 40°, the base of the exposure being about 2 feet above the usual high-tide mark. We dug away sufficient soil and vegetation to expose several square yards of fresh rock and made what seemed to be an adequate collection through a thickness of about 18 inches. There was apparently much more fossil-bearing rock available below, and extending upward, into the forested bank. Only two megafossils were present: *Chaleuria cirrosa* in great abundance and a few scattered fragments that probably represent a species of *Psilophyton*.

DESCRIPTION OF *CHALEURIA CIRROSA*, NEW GENUS AND SPECIES

General morphology. Two representative specimens of *Chaleuria cirrosa* are shown in Plates 52 and 53. Judging from such specimens the plant consisted of a main axis about 10 mm in diameter which was upright and has not been observed to dichotomize. These two specimens are slightly curved and the axes are found in some blocks to be aligned in more or less parallel rows. There is a suggestion that they may have been borne by a rhizomatous stem as, for example, in *Hyenia elegans* as recently described by Schweitzer (1972). We can only report that no such organ has been found and we will therefore refer to specimens such as those shown in Plates 52 and 53 as composed of a *main axis* bearing *primary branches*.

The main axis in most specimens is broken at both ends so that we do not know the maximum height that was attained. The greatest diameter of the main axis is a little over 1 cm, it shows little tapering, and it is our estimate that the plants attained a height of about 1 m. The main axis bears abundant primary branches in a very close spiral; numerous specimens were degaged to a greater or less degree and in all cases it was found that the primary branches are attached all around the main axis (text-fig. 2).

The primary branches are either entirely sterile (presumably photosynthetic) or entirely fertile; in some specimens the fertile branches are found at the lower part of the main axis (Pl. 53, arrow) but since the latter is not complete no more exact statement can be made concerning the relative position of fertile and sterile branches.

The sterile branches bear secondary (ultimate) branchlets, also in a close spiral, and they dichotomize once or twice with the terminations tending to recurve rather strongly (Pl. 54, figs. 1, 2). A few specimens show secondary branches which are monopodial and bear third-order ultimate branchlets.

The fertile primary branches (Pl. 54, fig. 6 and text-fig. 3) appear very similar to the sterile ones and likewise bear ultimate branchlets (Pl. 54, figs. 3–5) that dichotomize once or twice, and occasionally even three times, with a pair of sporangia at each ultimate, recurved branch ending. The sporangia are ovoid, measuring approximately 2.0 to 2.3 mm long and 0.6 to 0.7 mm broad.

The primary branches, sterile and fertile, are 2 to 3 mm in diameter at their proximal end and, like the main axis, the tips are lost; the longest ones are about 9 cm, but since the distal end is broken they may have been considerably longer. We have no positive evidence of dichotomy in the primary branches; if this did take place it was quite rare. The ultimate branchlets are up to 8 mm long and their axes 0.5 to 1.0 mm wide.

The restoration drawings (text-figs. 2, 3) give our impression of a representative part of the plant as it appeared in life. It certainly had a much denser or 'bushy' appearance than is gained from an examination of a freshly exposed specimen. As has been explained for the restoration drawings of *Pertica quadrifaria* (Kasper and Andrews 1972), only a small portion of a three-dimensionally branching plant of this kind is initially exposed.

Sporangia and Spores. The sporangia and their contained spores present the most significant aspect of our plant. Sporangia were degaged from fertile specimens which contained only *Chaleuria*. The first sampling included sporangia from several specimens while the second and third included sporangia from only one specimen. The sporangia selected for removal were attached to the plant and were removed with as little matrix as possible. All of the samples yielded essentially identical results.

The rock fragments containing sporangia were treated with hydrochloric acid, washed, and then macerated in hydrofluoric acid. The macerate was washed and the liberated sporangia and spore masses were extracted with a pipette, cleared in a mixture of potassium chlorate and nitric acid, washed and treated with dilute ammonium hydroxide. They were washed again and mounted on slides with a 1:1 mixture of Turtox CMC-9 and CMC-10 non-resinous mounting medium. Some sporangia and most spore masses were mounted on slides immediately after clearing and washing as the spore masses blackened when treated with the base. The sporangia were not obviously affected by the chemicals employed, but the spores showed varying degrees of corrosion, some probably caused by fossilization and some due to maceration.

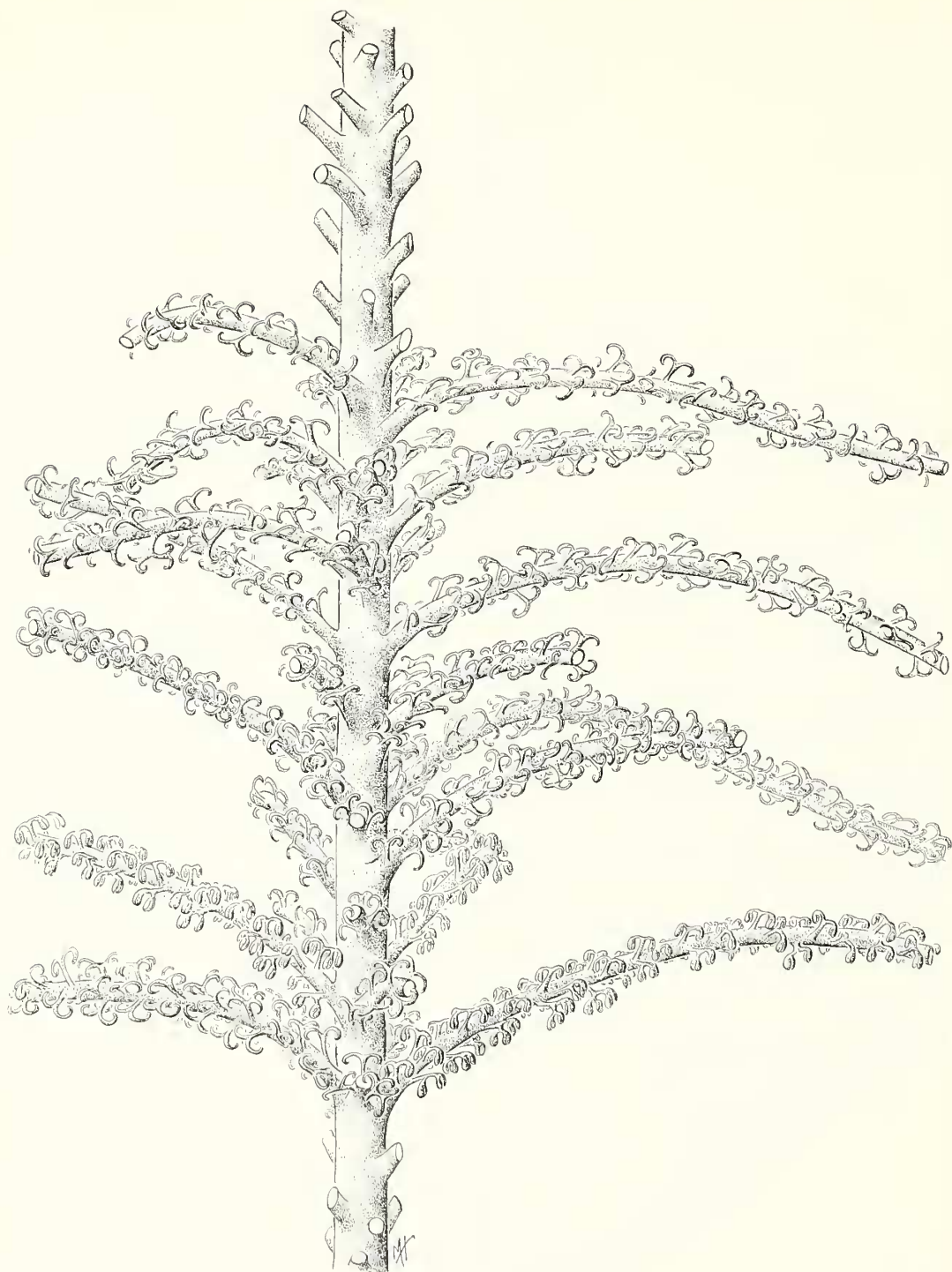
The sporangia extracted from the macerate ranged from whole ones to small fragments. Many apparently intact sporangia broke apart during the clearing process. The spore masses varied from large fragments with pieces of carbonized

EXPLANATION OF PLATE 52

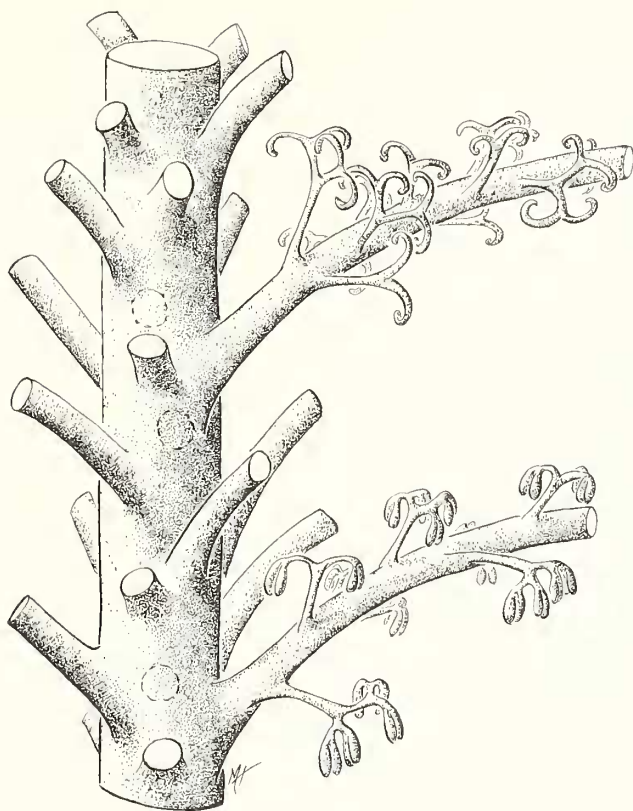
Chaleuria cirrosa. Specimen showing erect main axis and closely spaced, spirally arranged primary branches. Arrow indicates fertile ultimate branchlet borne near base of a primary branch. This is enlarged in Pl. 54, fig. 5. Type specimen No. 33258, $\times 1$. All specimen numbers are those of the Canadian Geological Survey.



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TEXT-FIG. 2. *Chaleuria cirrosa*. Restoration of a representative part of the plant showing the general habit.



TEXT-FIG. 3. *Chaleuria cirrosa*. Restoration of part of a plant showing the densely spiralled arrangement of the primary branches and portions of one fertile and one sterile primary branch in detail.

material adhering to them, and resembling fragmentary sporangia, to nearly uncarbonized spore masses of varying sizes. After clearing with Schulze's solution some spore masses were teased apart with a fine needle in order to better observe the spores. A few intact sporangia were also broken apart in the same manner; this proved difficult but a few sporangia were successfully teased apart and some of their spores spread out without being totally destroyed.

As a supplement to the usual microscopic study, selected individual spores were also examined and photographed with a Zeiss photomicroscope using Nomarski interference-contrast optics, which allows examination of external exine features by reflected light.

The sporangia. Plate 55, figs. 1 and 2 show sporangia that have discharged most of their spores before fossilization and reveal the form and wall structure quite well. The sporangia are fusiform to ovoid in shape and frequently curved (Pl. 55, fig. 1). A few of them remained paired when removed from the macerate but they usually separated

while clearing. An unseparated pair, consisting of a whole sporangium and part of another one, is illustrated in Plate 55, fig. 2.

The cells of the sporangium wall (Pl. 55, figs. 1, 2) are polygonal and randomly arranged. Globules of what appears to be tapetal material are scattered over the wall cuticle and outline individual cells. Many of the sporangia are split open at the distal end or throughout the entire length, indicating that dehiscence occurred longitudinally, starting at the tip. No specialized annulus cells have been observed.

Many sporangia or fragments of sporangia were recovered which retained their entire spore mass or varying portions of the original content; in addition the maceration process left fragmentary spore masses from which the sporangium wall had more or less disintegrated. The entire spore masses usually did not clear satisfactorily, probably having been immature at the time of fossilization. Thus our information is based chiefly on partially filled sporangia and portions of spore masses where we are reasonably certain that the spores are mature.

As the photographs reveal (Pls. 55-57) there is a remarkable variation in spore size, but for the most part they fall within two size ranges: some sporangia contain small spores 30 to 48 μm in diameter (Pl. 55, fig. 3) while others contain significantly larger spores ranging from 60 to 156 μm in diameter (Pl. 55, fig. 4). The sporangia containing predominantly small spores may include a few larger ones and the small spores may be present in sporangia with large spores; this kind of association was observed frequently enough to convince us that it is significant and not a matter of contamination.

The small spores are morphologically similar to one another and they differ in both size and ornamentation from the larger ones. The larger (mega-) spores are more varied in both size and morphology than the smaller (micro-) spores; plotting the size distribution of 50 large spores (taken from several sporangia) reveals two peaks, one at 60 to 75 μm and one at 120 to 130 μm . The two spore groups will be dealt with individually for a more detailed description.

The large spores. The large spores (Pl. 56, figs. 1-4), ranging from 60 to 156 μm in diameter, are trilete and circular to subcircular in outline. The exine varies from 1 to 6 μm thick, the largest spores being thinner (1-3 μm) than the smaller ones. Most of them possess distinct contact areas extending about two-thirds of the spore radius and delimited by curvaturae. The contact areas are either smooth or bear a reduced sculpture. The smaller spores have a very sinuous triradiate mark (Pl. 56, figs. 1, 2) while some of the larger ones have slightly wavy to straight rays with varying degrees of lip development (Pl. 56, figs. 3, 4); the triradiate mark extends about one-half to two-thirds the spore radius and the rays are usually raised by folds 3 to 6 μm wide. The exine outside the contact areas on the large spores is sculptured with closely packed minute granules or rods (rarely cones) which are from 0.5 to 1.5 μm high and half as wide as high.

EXPLANATION OF PLATE 53

Chaleuria cirrosa. Specimen showing general habit. Primary branch at arrow shows spirally arranged fertile ultimate branchlets. This is enlarged in Pl. 54, fig. 6. No. 33259, $\times 1$.



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The small spores (Pl. 55, fig. 3; Pl. 56, figs. 5, 6; Pl. 57, figs. 1, 2, 3, 5). These are 30 to 48 μm in diameter (50 specimens measured), are trilete, and subtriangular to triangular in outline. The exine is 1 to 2 μm thick; it may be uniform or slightly thinner proximally. The triradiate mark is distinct and simple or bordered by narrow lips or folds 1 to 2 μm wide; the latter may merge with the contact areas. The straight rays extend three-quarters to seven-eighths of the spore radius. The proximal face is smooth and often has distinct contact areas surrounded by folds or by a thickening, either of which nearly coincides with the equatorial margin. A few spores observed in lateral compression exhibit very clearly a thickening delimiting the contact areas which can be interpreted as *curvaturae perfectae*. A small percentage of spores appear to lack *curvaturae* or distinct contact areas; these often also have a uniformly thick exine and are more than 40 μm in diameter.

The exine outside the contact areas is sculptured with baculi, coni and rarely spinae; these elements are from 1.5 to 3.0 μm high and 0.5 to 1.5 μm wide at the base. The cones are broad-based, taper abruptly to fine points, and are occasionally biform, curved or anastomosing to form short ridges. The baculi are fine and straight. The sculptural elements are widely spaced, sometimes 2 to 3 μm apart and the cones and baculi rarely occur together on the same spore.

'Other' spores. Most of the small-spore masses include a few spores that are identical to the large type. In addition, two other kinds of larger bodies were observed. One is an apparent spore lacking a trilete mark but sculptured with anastomosing, wart-like elements tipped by small cones; one or two of these are constantly present in the small-spore masses. Another spore-like structure has been observed associated with both the small and large spores. These are large, thin-walled, transparent bodies (Pl. 57, figs. 6, 7) that lack a trilete mark and several were observed with small spores inside; it is possible that these structures represent a persisting mother-cell wall.

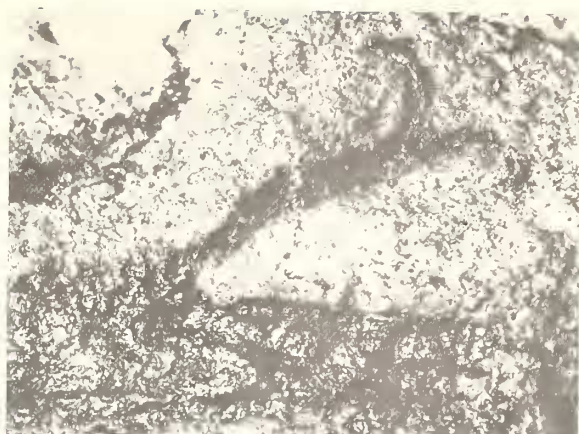
Dispersed spores. Although we are not primarily concerned with the palynology of the sediments a bulk maceration of several rock fragments was prepared chiefly as an aid in interpreting the problematical spores found associated with our 'small' and 'large' types. For the most part we obtained only sporangial fragments and spores of *Chaleuria*. A few spores of *Emphanisporites* (cf. *R. rotatus* McGregor) were found and a reticulum fragment possibly referable to *Brochotriletes*. We feel

EXPLANATION OF PLATE 54

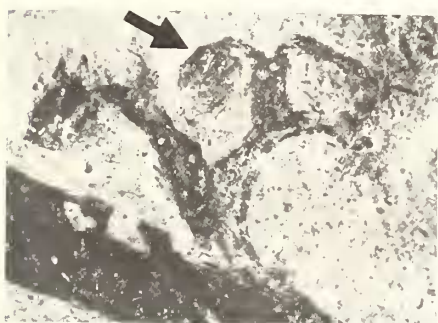
Figs. 1-6. *Chaleuria cirrosa*. 1, sterile ultimate branchlet with at least one dichotomy and strongly recurved tip. 'B' indicates primary branch; arrow points to first dichotomy of ultimate branchlet. No. 33258, $\times 7$. 2, sterile ultimate branchlet with one dichotomy visible. No. 33260, $\times 9$. 3, fertile ultimate branchlet showing at least two divisions and a possible third one. Arrow points to a terminal pair of sporangia. No. 33261, $\times 6.5$. 4, two ultimate fertile branchlets; arrows indicate sporangial pairs. No. 33262, $\times 6.5$. 5, fertile ultimate branchlet; this is indicated by arrow in Pl. 52. Lower arrow points to dichotomy of the branchlet; upper arrow indicates one sporangium of a pair. No. 33258, $\times 5$. 6, enlargement of fertile primary branch shown by arrow in Pl. 53. Several fertile ultimate branchlets bearing terminal pairs of sporangia are evident. No. 33259, $\times 4$.



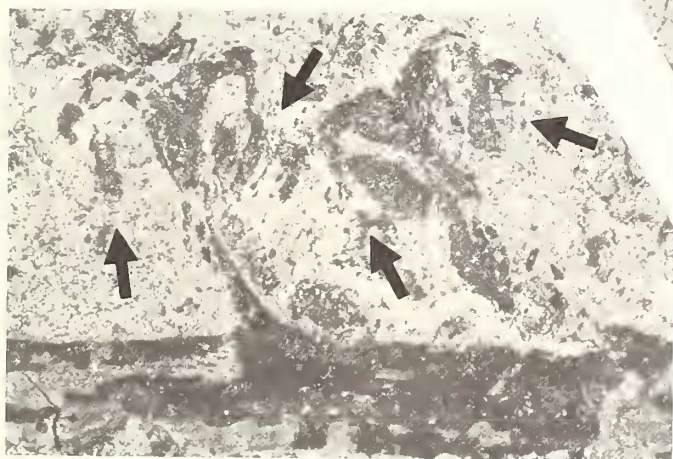
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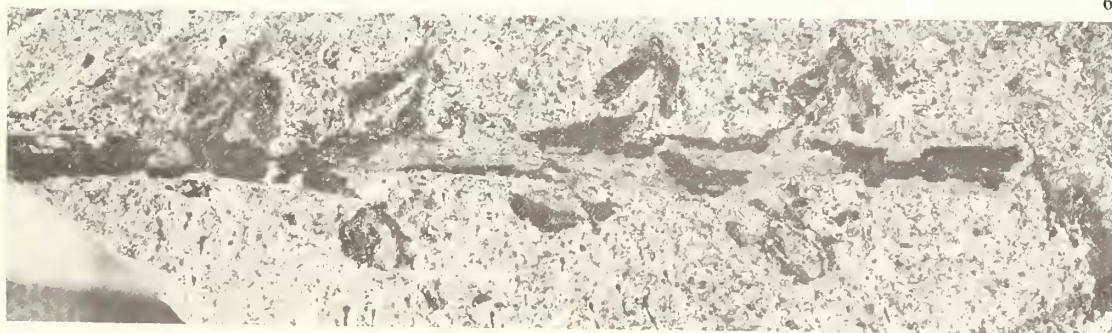
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6

that this paucity of dispersed spores in the rock matrix strongly supports our supposition that the 'odd type' spores contained in some sporangia are not contaminants.

DIAGNOSTIC DATA

CHALEURIA Andrews, Gensel, and Forbes, gen. nov.

Diagnosis. Plants with erect main axis bearing closely spaced, spirally arranged primary branches. Primary branches monopodial, either sterile or fertile, with closely spaced, spirally arranged dichotomous ultimate branchlets. Distal divisions of ultimate branchlets recurved; those of fertile ones terminated by pairs of ovoid sporangia. Occasionally a third order of branching present. Sporangia ovoid, with morphologically distinct spores of two sizes.

Chaleuria cirrosa Andrews, Gensel, and Forbes, sp. nov.

Diagnosis. As in generic diagnosis. Plants with main axes up to 1 cm wide, probably up to 1 m tall in life. Sterile and fertile primary branches 2–3 mm wide at the base, up to 9 cm long. Ultimate branchlets 1–2 and rarely 3 times dichotomous, up to 8 mm high, individual axes 1 mm or less in width, tips strongly curved. Fertile ultimate branchlets with pairs of ovoid sporangia 2–2.5 mm long, 0.6–0.7 mm wide. Dehiscence longitudinal, no annulus. Sporangia with trilete spores of two sizes and distinct morphologies. Large spores 60–156 μm in diameter, circular to subcircular in outline. Exine 1–6 μm thick. Contact areas distinct to barely discernible, smooth or with reduced sculpture; where distinct, delimited by *curvaturae perfectae*. Distal exine sculptured with closely packed grana or baculi 0.5–1.5 μm high. Triradiate mark $\frac{1}{2}$ to $\frac{2}{3}$ spore radius, straight to sinuous, simple or with lips. Small spores 30–48 μm in diameter, triangular to subtriangular in outline. Exine 1–2 μm thick, usually thinner proximally. Proximal hemisphere smooth, usually with contact areas delimited by folds or a thickening nearly coinciding with the equator. Distal hemisphere and equatorial margins sculptured with baculi or broad-based, sometimes bifiform con. Sculptural elements 2–3 μm apart, 1–3 μm high. Triradiate mark simple, with lips or with folds 1–2 μm wide, rays extend $\frac{3}{4}$ to $\frac{7}{8}$ spore radius.

Derivation of the name. The generic name *Chaleuria* is taken from the general locality, Chaleur Bay, New Brunswick. The specific epithet *cirrosa* is derived from the Latin word *cirrosus* meaning 'full of curls' in reference to the recurved tips of the ultimate branchlets.

Deposition of specimens. The type specimens and other specimens and slides illustrated will be deposited in the collections of the Canadian Geological Survey, Ottawa.

EXPLANATION OF PLATE 55

Figs. 1–4. *Chaleuria cirrosa*. 1, a cleared sporangium showing cellular structure of wall, stalk (above), and split-open tip (below). No. 33264, $\times 45$. 2, pair of sporangia, one only partially intact. No. 33264, $\times 45$. 3, part of a mass of predominantly small spores. No. 33265, $\times 280$. 4, part of a spore mass from a sporangium containing the large spores of variable size. Arrow indicates spores in the 60–80 μm range. No. 33263, $\times 280$.



Holotype. Specimen No. 33258—Plate 52, fig. 1.

Paratypes. Specimen No. 33259—Plate 53, fig. 1.

Slide No. 33264—Plate 55, figs. 1, 2.

Slide No. 33265—Plate 56, figs. 5, 6; Plate 57, figs. 1, 2; Plate 55, fig. 3.

Locality. Beach outcrop three-quarters of a mile west of Dalhousie Junction, New Brunswick, Canada. Point 'A' on map in text-fig. 1.

Horizon. Campbellton Formation, Gaspé Sandstone; probably Middle Devonian.

DISCUSSION

Comparison with other megafossils. There are few Devonian megafossils with which we are able to draw a very close comparison with *Chaleuria*. *Hyenia elegans* Krausel and Weyland, as described by Schweitzer in 1972, presents some comparable features. This lower Middle Devonian plant from the Rhineland consists of a rhizome about 4 cm in diameter with upright shoots borne all around the rhizome in a close phyllotaxy; the aerial shoots branch quite profusely developing a crown-like pattern which is unlike our plant. The ultimate fertile appendages seem nearly identical to those of *Chaleuria* but the sterile ones are not. Preserved spores are not reported in Schweitzer's account.

Arctophyton gracile, described by Schweitzer (1968) from the lower Middle Devonian of Spitzbergen, is quite closely comparable to *Chaleuria* in its general habit and in the morphology of the sporangiate appendages; the ultimate sterile appendages of *Arctophyton* are in part somewhat more profusely branched. It is unfortunate that the sporangial contents of this Arctic plant are not preserved.

Comparison with dispersed spore genera. Large spores: the large *Chaleuria* spores fit the emended concept of the dispersed spore genus *Apiculiretusispora* Streeel (Streeel 1967), but are not identical with any of the presently described species. *Chaleuria* spores like the one illustrated in Plate 56, fig. 3 have some similarities with *A. brandtii* Streeel (1964) and *A. plicata* (Allen) Streeel (1967). *A. brandtii* differs, for the most part, in having a darkened apical area and simple trilete mark, and *A. plicata* is smaller and has a thinner exine.

The large *Chaleuria* spores like those illustrated in Plate 56, figs. 1, 2 are strikingly similar to *Cyclogranisporites flexuosus* Playford (1962), from the Lower Carboniferous. Similar spores have been described from the Lower and Middle Devonian by Schultz (1968) and Lanninger (1968). Both *C. flexuosus* and the large *Chaleuria* spores referred to above are of similar size and all of them exhibit a raised sinuous

EXPLANATION OF PLATE 56

Figs. 1-6. *Chaleuria cirrosa*. All figures at $\times 640$.

Figs. 1-4. Large spores, showing variation in size and morphology. These are not from one sporangium but comparable spores have all been observed in one sporangium. 1, 2, large spores with distinct contact areas and sinuous triradiate rays. 1, No. 33267. 2, No. 34597. 3, large spore with less prominent contact areas and straighter rays. No. 33266. 4, thin-walled, probably corroded, large spore with barely discernible contact areas. Sporangium wall overlies spore. No. 33264.

Figs. 5-6. Small spores. 5, proximal view showing curvaturae. 6, distal view of same spore. No. 33265.



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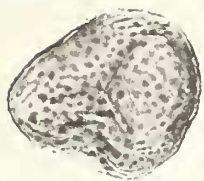
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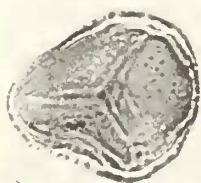
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triradiate mark, a distal sculpture of small elements (grana) and, for the most part, distinct contact areas which are either smooth or bear a reduced sculpture. A small difference between spores of *C. flexuosus* and the large *Chaleuria* spores is that in the former the contact areas are not always as distinct or curvaturate as in the large *Chaleuria* spores.

A single spore described and illustrated by de Jersey (1966) from the Middle Devonian of Australia as *Retusotriletes* sp. cf. *R. devonicus* Naumova is quite similar to some of the large *Chaleuria* spores. The largest of the large *Chaleuria* spores which do not possess distinct contact areas or curvaturae agree with the concept of the genus *Cyclogranisporites*.

Small spores: the small spores of *Chaleuria* resemble several dispersed spore genera but many of the spores observed fit most closely the concept of the genus *Streelispota* Richardson and Lister (1969) in possessing an equatorial crassitude which delimits contact areas, distal sculpturing of various kinds of elements and a smooth proximal face. *S. newportensis* (Chaloner and Streel) Richardson and Lister (1969) is most similar to the small *Chaleuria* spores but differs from them in possessing papillae and folds on the proximal facets, more robust-appearing cones and in lacking baculi.

Streelispota is very close to, or possibly congeneric with, the genus *Aneurospora* Streel (1964). At present the nature of the curvaturae of the two separates them, the curvaturae of *Streelispota* corresponding to an equatorial crassitude and the curvaturae of *Aneurospora* being still interpreted by Streel (1972) as a denser, more rigid part of the exine. The small *Chaleuria* spores differ at present from *Aneurospora* therefore in the nature of their curvaturae and also in having a thinner proximal exine and a thicker distal one. The ornamentation of *A. goensis*, the species that is most closely comparable to the small *Chaleuria* spores, is also finer than that of the small *Chaleuria* spores.

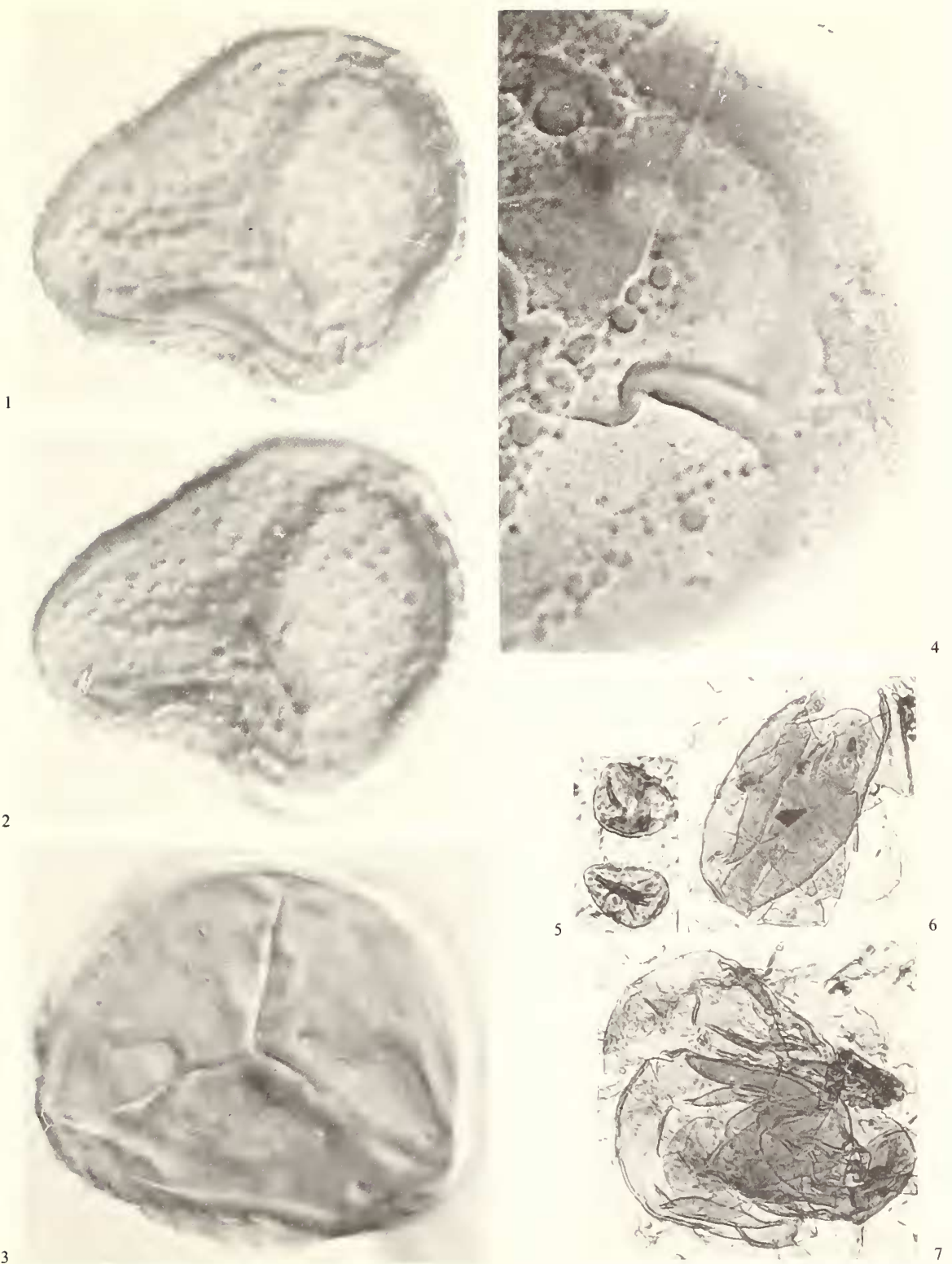
The small *Chaleuria* spores in which curvaturae are not apparent resemble in some aspects the genus *Procoronospora* Butterworth and Williams. *P. dumosus* (Staplin) Smith and Butterworth (1967) appears similar to the small *Chaleuria* spores but has an ornamentation of fairly long spines and a uniformly thick exine. A spore identified as cf. *Procoronospora*, from the Emsian of Ontario, Canada, in McGregor *et al.* (1970) is quite similar to some of the small *Chaleuria* spores but a description was not included. Another, cf. *Procoronospora* sp., is illustrated in McGregor and Owens (1966) from the Emsian of the Gaspé which also appears similar to the small *Chaleuria* spores. Most of the small *Chaleuria* spores differ from the concept of

EXPLANATION OF PLATE 57

Figs. 1-7. *Chaleuria cirrosa*.

Figs. 1-4. Spores photographed with Nomarski interference-contrast optics. All at $\times 1600$. 1, 2, small spores illustrated in Pl. 56, figs. 5, 6. Proximal and distal focus respectively with sculpture visible especially well along margins. 3, small type spore with corroded exine, but showing smooth proximal face and curvaturae. No. 34596. 4, large spore illustrated in Pl. 56, fig. 1, showing part of contact areas.

Figs. 5-7. Spores found within a single sporangium. No. 33263. All at $\times 280$. 5, two small spores. 6, 7, large, problematical thin-walled bodies (spore mother cell wall?). Several small spores are present within in Fig. 7.



Procoronospora in possessing *curvaturae*, and in not always exhibiting the characteristic absence of ornamentation at the radial margins. Finally, some of the small *Chaleuria* spores resemble *Anapiculatisporites burnotensis* Streel (1967) except that the latter lacks *curvaturae*.

In summary, a comparison of possibly related megafossils and dispersed spores with *Chaleuria cirrosa* suggests that the latter is not younger than Middle Devonian in age.

The evidence for heterospory in Chaleuria. Two sizes of morphologically distinguishable spores have been described for *Chaleuria* that have been found in cleared and uncleared sporangia, in spore masses, and also have been removed from sporangia by teasing with a needle. Our evidence suggests that these two sizes of spores are either intermixed in a sporangium or occur separately in different sporangia.

As noted above the only megafossils that were associated with our collections of *Chaleuria cirrosa* were a few sterile axes that might belong to a *Psilophyton* species. On this basis it is unlikely that the sporangia and spore masses that we have described belong to any other plant. Several of our specimens are fertile and in our initial investigation of the sporangia we degaged them from several specimens; some of the sporangia thus obtained were observed to be attached while others may have been buried in the matrix. Upon macerating them the results were obtained as described above. As a check we studied a second series of macerations in which all of the sporangia were obtained from a single specimen. It is not certain that all of these came from one plant but they did come from fertile branches of *Chaleuria*. A third, and seemingly conclusive, bit of evidence that all of the described material is correctly attributed to the plant, lies in the sporangia themselves. Although there are some slight size differences they are all essentially identical in form and cell wall structure.

Sussex (1966) has prepared a very informative discussion on 'The origin and development of heterospory in vascular plants' and it is therefore unnecessary for us to review the subject in detail; we will consider only such facets of the matter as seem pertinent to an understanding of *Chaleuria*.

We would, of course, like to know what happened to the spores of *Chaleuria* when they germinated. Although this cannot be done directly, we do have what seems to be a closely comparable phenomenon in a living fern, *Platyzoma microphyllum* Robert Brown. The evolution of heterospory has taken place in numerous pteridophytic lines and at different times in the geologic past; it appears in several groups in the late Devonian and Lower Carboniferous (Andrews 1961; Chaloner 1967; Sussex 1966) but the case of *Platyzoma* suggests that it is not a biological event that is confined to the distant past. *P. microphyllum* is a Queensland plant that has attracted the attention of several investigators during the past century. Although originally placed in the Gleicheniaceae by Brown it has more recently been assigned to a new subfamily (Platyzomatoideae) of Christensen's Polypodiaceae by Tryon (1961, 1964). Of special interest in the present context are features of its sporangia. These vary in size and in the orientation of the annulus and the contained spores show a considerable size range (Thompson 1916, 1917); it seems pertinent to consider them in some detail.

In his 1917 account Thompson notes that 'The large sporangia contained small numbers of large spores, the small sporangia larger numbers of small spores' (p. 158). In two tables on pages 162 and 163 he shows that the sporangia that contain predominantly small spores may contain a few of the large and/or intermediate size spores; likewise those sporangia that contain predominantly large spores may also contain a few of the small and/or intermediate ones. In her more recent study Tryon (1964) gives a range in size for the small spores of 71 to 101 μm and she showed that these produce a filamentous gametophyte-bearing antheridia; the large spores range from 163 to 183 μm and produce larger, spatulate gametophytes that bear archegonia. In a personal communication she has informed us that she also observed spores intermediate between the small and large ones but information is not available on the nature of the gametophytes they produce.

The lycopods present another analogy that seems relevant and deserves at least a brief comment. In the Carboniferous members of the group the well-preserved cones of *Lepidostrobus* and *Lepidocarpon* show the most complete sequence that we have in the evolution of heterospory. Starting with a lower Mississippian species there is a reduction in the number of megaspores per sporangium, an increase in the size of the remaining megaspores, and in *Lepidocarpon*, where only one functional spore remains, the megasporangium is partially enclosed by the sporophyll to form a seed (Andrews 1961, pp. 231–232). In the living *Selaginellas* there is considerable variation, in several species, in the number and size of the megaspores per sporangium (Duerden 1929). For example, in *Selaginella willdenowii* Baker, Duerden reports a range of from one to as many as 42 megaspores in a sporangium. One of his summary comments seems to have a very direct bearing on what we have found in *Chaleuria*: 'The occurrence in *Selaginella* of megasporangia containing many comparatively small spores, suggests a condition possibly not far advanced beyond the homosporous state, and, on the other hand, the sporangia with fewer, comparatively large spores, indicates an advance in the direction of the seed habit' (p. 456).

To the best of our knowledge *Chaleuria* is the oldest megafossil that is sufficiently well preserved to understand its gross morphology and in which the sporangia and spores present adequate evidence to indicate heterospory. A few other plants deserve discussion which seem to support our stand and which contribute to this very important phase in vascular plant evolution. One of the oldest genera in which heterospory is known is *Barinophyton* and in his review (Pettitt 1970) of the early evidences of heterospory Pettitt cited *B. richardsoni* (Pettitt 1965) from the Frasnian (lower Upper Devonian) of Maine and *B. citrulliforme* (Arnold 1939) from the Famennian (upper Upper Devonian) as being heterosporous. He also notes (1970, p. 404) that plants with a habit similar to *Barinophyton* have been reported from sediments older than the Upper Devonian but either the spores are not known or they have not been shown to be heterosporous. Pettitt also briefly mentions (1970, p. 405, pl. 4, fig. 2) an undescribed Emsian (upper Lower Devonian) plant from New Brunswick in which the spores range from 97 to 240 μm . No other information is available and judging from his figure the plant is not closely related to *Chaleuria*. He offers the following comment on the New Brunswick plant in question: 'Clearly, an evolutionary situation in heterospory which we would expect to find in a particular line would be an incipient condition presaging a later and more definite distinction

between microspore and megaspore' (p. 405). We do not offer an opinion on the plant that Pettitt's comment is based on but *Chaleuria* seems to fit very nicely this concept of incipient or primitive heterospory.

Several other fossil plants present apparently comparable primitive stages in heterospory. *Protopitys scotica* Walton, according to Walton's description (1957), bears sporangia with three kinds of spores; in some sporangia the spores are about 82 μm , others contain spores that are 147 μm , while a few have spores that are 98 μm . In a later report on this plant Smith (1962a) concluded that the spores fall within two, rather than three, sizes but there is, nevertheless, a considerable range, from 75 to 355 μm . In another Lower Carboniferous plant (*Staphylothea kilpatrickensis*) Smith (1962a) described two kinds of spores, one ranging from 42 to 57 μm and the other ranging from 78 to 100 μm in diameter; these two, along with a third 'type' that is regarded as immature, occur in the same sporangium. He does not mention the possibility of heterospory. In a third lower Carboniferous plant, *Alcicornopteris hallei* Walton, Smith (1962b) described four different kinds of spores, the differences being more in gross morphology and exine structure than in size, with the overall range being 50 to 130 μm .

These selected examples of both living and fossil plants, representing several divergent groups, afford a considerable amount of consistent evidence bearing on the evolution of heterospory. Apparently the segregation of two distinct types of spores, relative to size and sexual differentiation, evolved gradually. The smaller spores germinate to form male gametophytes and the larger ones to form female gametophytes and to date we have little information on the function of the intermediate types.

Accordingly, we feel that it is highly probable that the same pattern applies to *Chaleuria cirrosa*, that the small and large spores produced male and female gametophytes respectively, and we suggest that some of the intermediate ones formed bisexual gametophytes.

The classification of Chaleuria cirrosa. We are not able to fit *Chaleuria* satisfactorily into any existing scheme of classification. The problem is aggravated by a common one in palaeobotany, that is, lack of data comparable with those available in other plants. Several otherwise rather well-known Lower and Middle Devonian plants might bear comparison except they lack the preservation of the sporangiate organs that we do have in *Chaleuria*.

Probably the closest comparison that we can make on the basis of general morphology is with *Arctophyton gracile* Schweitzer from the Middle Devonian of Spitzbergen. Schweitzer refers to it as '... probably a fern or a "progymnosperm" related to *Aneurophyton*'.

It is our opinion that the 'main stream' of plant evolution leading to the Pteridosperms runs in a general way from very simple plants such as *Psilophyton* through increasingly complex types such as *Pertica*, *Rhacophyton*, and *Archaeopteris*. We do not imply a straight-line series but rather suggest these genera as showing stages in the evolution of a laminate megaphyll, the cambium and heterospory.

It is now clear that the early land plants of the Lower Devonian evolved into a rather diverse assemblage by Middle Devonian times. Some of the latter ran into

blind alleys or evolved into true ferns (Filicales and Marattiales), others led to the problematical and heterogeneous Coenopterids, and others led toward the Progymnosperms, which we are just beginning to understand. On the basis of apparent heterospory we tentatively regard *Chaleuria* as a primitive member of the Progymnosperms.

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REFERENCES

- ALCOCK, F. J. 1935. Geology of Chaleur Bay Region. *Mem. geol. Surv. Can.* **183**, 146 pp.
- ANDREWS, H. N. 1961. *Studies in Paleobotany*. John Wiley and Sons, New York. 487 pp.
- ARNOLD, C. A. 1939. Observations on fossil plants from the Devonian of eastern North America. IV. Plant remains from the Catskill Delta deposits of northern Pennsylvania and southern New York. *Contrib. Mus. Paleont. Univ. Mich.* **5**, 271–313, 10 pls.
- CHALONER, W. G. 1967. Spores and land-plant evolution. *Rev. Palaeobot. Palynol.* **1**, 83–93.
- CHANDLER, M. E. J. 1964. The Lower Tertiary Floras of Southern England. IV. A summary and survey of findings in the light of recent botanical observations. *Brit. Mus. Nat. Hist.* 151 pp., 4 pls.
- DE JERSEY, N. J. 1966. Devonian spores from the Adavale Basin. *Publs. geol. Surv. Qd.* (Palaeontological Papers No. 3), **334**, 1–28, 10 pls.
- DUERDEN, H. 1929. Variations in megaspore number in *Selaginella*. *Ann. Bot.* **43**, 451–457.
- KASPER, A. E. and ANDREWS, H. N. 1972. *Pertica*, a new genus of Devonian plants from northern Maine. *Am. J. Bot.* **59**, 892–911.
- LANNINGER, E. P. 1968. Sporen-Gesellschaften aus dem Ems der SW Eifel (Rheinisches Schiefergebirge). *Palaeontographica*, **B 122**, 95–170, pls. 20–26.
- MCGREGOR, D. C. and OWENS, B. 1966. Devonian spores of eastern and northern Canada. *Pap. geol. Surv. Can.* **66-30**, 1–66, 29 pls.
- SANFORD, B. V. and NORRIS, A. W. 1970. Palynology and correlation of Devonian formations in the Moose River Basin, Northern Ontario. *Proc. geol. Ass. Can.* **22**, 45–54, 2 pls.
- PLAYFORD, G. 1962. Lower Carboniferous Microfloras of Spitsbergen. Part I. *Palaeontology*, **5**, 550–618, pls. 78–87.
- PETTITT, JOHN M. 1965. Two heterosporous plants from the Upper Devonian of North America. *Bull. Brit. Mus. (nat. Hist.)* (Geol. & Miner.), **10**, 83–92, 2 pls.
- 1970. Heterospory and the origin of the seed habit. *Biol. Rev.* **45**, 401–415, 6 pls.
- RICHARDSON, J. B. and LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201–252, pls. 37–43.
- SCHULTZ, G. 1968. Eine Unterdevonische mikroflora aus den Klerfer Schichten der Eifel (Rheinisches Schiefergebirge). *Palaeontographica*, **B 123**, 5–42, pls. 1–4.
- SCHWEITZER, H.-J. 1968. Pflanzenreste aus dem Devon Nord-Westspitsbergens. *Ibid.* **B 123**, 43–75, pls. 5–15.
- 1972. Die Mitteldevon-Flora von Lindlar (Rheinland). 3. Filicinae-*Hyenia elegans* Krausel and Weyland. *Ibid.* **B 137**, 154–175, pls. 30–39.
- SMITH, A. H. V. and BUTTERWORTH, M. A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Spec. Pap. Palaeont.* **1**, 324 pp., 27 pls.
- SMITH, D. L. 1962a. Three fructifications from the Scottish Lower Carboniferous. *Palaeontology*, **5**, 225–237, 2 pls.
- 1962b. The spores of *Alcicornopteris hallei* Walton. *Ann. Bot. N.S.* **26**, 267–277, 1 pl.
- STREEL, M. 1964. Une association de spores du Givetien Inférieur de la Vesdre. *Ann. Soc. geol. Belg.* **87**, 1–30, 2 pls.
- 1967. Associations de spores du Dévonien Inférieur Belge et leur signification stratigraphique. *Ibid.* **90**, 11–54, 5 pls.
- 1972. Dispersed spores associated with *Leclercquia complexa* Banks, Bonamo and Grierson from the late Middle Devonian of eastern New York State (U.S.A.). *Rev. Palaeobot. Palynol.* **14**, 205–215, 2 pls.

- SUSSEX, I. M. 1966. The origins and development of heterospory in vascular plants. In E. G. CUTTER (ed.), *Trends in Plant Morphogenesis*. John Wiley and Sons, New York. Pp. 140-152.
- THOMPSON, J. M. 1916. The anatomy and affinity of *Platyzoma microphyllum* R. Br. *Trans. roy. Soc. Edinb.* **51**, 631-656.
- 1917. A further contribution to the knowledge of *Platyzoma microphyllum* R. Br. *Ibid.* **52**, 157-165.
- TRYON, A. F. 1961. Some new aspects of the fern *Platyzoma microphyllum*. *Rhodora*, **63**, 91-102.
- 1964. *Platyzoma*—A Queensland fern with incipient heterospory. *Am. J. Bot.* **51**, 939-942.
- HALTON, J. 1957. On *Protopitys* (Goeppert): with a description of a fertile specimen '*Protopitys scotica*' sp. nov. from the Calcareous Sandstone Series of Dunbartonshire. *Trans. roy. Soc. Edinb.* **68**, 333-340, 3 pls.

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